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Governor

FUNCTIONAL COMPARISON BETWEEN PREDICTIONS OF A CHINOOK SALMON MODEL AND MONITORING DATA IN THE TUOLUMNE RIVER, CALIFORNIA

PIER FINAL PROJECT REPORT

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Table of Contents

List of Figures

List of Tables

Preface

The Public Interest Energy Research (PIER) Program supports public interest energy research and development that will help improve the quality of life in California by bringing environmentally safe, affordable, and reliable energy services and products to the marketplace.

The PIER Program, managed by the California Energy Commission (Energy Commission), conducts public interest research, development, and demonstration (RD&D) projects to benefit electricity and natural gas customers.

The PIER program strives to conduct the most promising public interest energy research by partnering with RD&D entities, including individuals, businesses, utilities, and public or private research institutions.

PIER funding efforts are focused on the following RD&D program areas:

- Buildings End-Use Energy Efficiency
- Energy-Related Environmental Research
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- Renewable Energy Technologies
- Transportation

Functional Comparison between Predictions of a Chinook Salmon Model and Monitoring Data in the Tuolumne River, California is the final report for the Testing and Improvement of the ORCM Chinook Salmon Model project (contract number 500-02-004, MR035) conducted by Oak Ridge National Laboratory. The information from this project contributes to PIER's Energy-Related Environmental Research program.

For more information about the PIER Program, please visit the Energy Commission's website at www.energy.ca.gov/pier/ or contact the Energy Commission at 916-654-5164.

Abstract

This study sought to reduce uncertainty in estimates of Chinook salmon outmigration in the Tuolumne River, California by (1) improving rotary screw trap (RST) estimates, and (2) improving predictions of a particular salmon recruitment model, the Oak Ridge Chinook Model (ORCM). The research team improved estimates of outmigrants based on RST monitoring data and developed methods for evaluating ORCM predictions by comparing relationships between model predictions and environmental covariates (referred to here as "functional relationships") with relationships between RST monitoring data and environmental covariates. This report presents methods for comparing model predictions with field estimates that can be used with data series that are autocorrelated and have gaps. Our model-data comparison suggested two hypotheses. The first hypothesis is that the density dependent mortality is weaker in the model than in the field. Examination of seining estimates of fry abundance could determine whether this mortality occurs during incubation or during the fry stage. The second hypothesis is that fish kills resulted in lower-than-predicted juvenile survival in years 2000–2004. This hypothesis could be addressed by examining this period for extreme river conditions. Finally, the capability to simulate energy generation was added to the ORCM, enabling it to quantify the effect of flow regime on both salmon and energy.

Keywords: functional comparison, time series, Chinook salmon, energy generation, rotary screw trap

Executive Summary

Introduction

Resource agencies in California and water agencies that generate hydropower are interested in better understanding how their decisions about seasonal and annual patterns in river flow will influence salmon production. The financial problems and energy deficits experienced by California during the late 1990s highlight the importance of understanding the loss of energy capacity associated with legal restrictions on flows. Better tools are needed to quantify the costs and benefits associated with hydropower production in California.

Purpose

Several models have been developed to predict the effects of hydropower operations on Chinook salmon production in California rivers, but have not had the opportunity to undergo a rigorous, iterative process of comparing predictions against field data, followed by model refinement and also improved collection and/or interpretation of field estimates. For example, when the Oak Ridge Chinook Model (ORCM) was developed in the mid-1990s, there was no program to monitor outmigrating Chinook salmon in the Tuolumne River. Since then, rotary screw trap (RST) data have been collected in this river and used to estimate salmon production. However, the true numbers of outmigrants are uncertain due to the low sampling efficiencies of RST data. The original purpose of this project was to develop and apply methods to compare predictions of an existing model with new field data, with the goal of reducing uncertainty in both model predictions and field-based estimates. This study's primary tool was a constructive "validation" that seeks to explain model-data discrepancies via empirical models involving environmental covariates.

Project Objectives

The three goals of this project were to: (1) improve methods for estimating numbers of outmigrating juveniles from RST data, (2) reduce uncertainty in ORCM predictions, and (3) add the capability to estimate hydropower generation in ORCM, which will allow users to determine the trade-offs between providing flows for energy production and providing flows for salmon habitat

Project Outcomes

The following five project outcomes are highlighted:

1. Two methods for improving estimated production based on RST data are presented.
2. Methods and tools for functional comparison between model predictions and field monitoring-based estimates are presented. These robust methods work for missing data and time series data that are autocorrelated.
3. Future directions for improving ORCM predictions during some years are recommended based on functional model-data comparisons. Results suggest

differences may be due to higher density dependent mortality than simulated or to episodes of poor water quality with effects not represented adequately in the model.

4. ORCM now has the added capability to simulate energy generation, which will permit the simultaneous evaluation of the effects of flow regimes on production of salmon and energy.
5. The analyses presented illustrate the value of continued feedback between environmental monitoring design and predictive model development. Such an iterative process is an essential part of effective adaptive management.

Conclusions

Empirical modeling proved useful as a tool for imputing missing field measurements and functional validation of a Chinook salmon model, ORCM. The timing of smolt outmigration was similar between model and data. However, ORCM predictions of smolts per spawner were much higher than RST-based estimates for some years. Our analysis suggested two hypotheses to explain the differences in juvenile survival. Thus, a longer process of monitoring, comparison, and refinement is needed (including a longer time series of field data, preferably with higher capture efficiencies) to improve our understanding of salmon smolt production in this river and to reap the benefits of the ORCM model as a predictive tool.

Benefits to California

Providing environmentally sound energy and reliable energy are two goals furthered by this research. This project started the process of testing and improving a model for quantifying the change in Chinook salmon production and the change in hydropower generation associated with regulated flow regimes. Results from this study could be used in the future to consider maximizing both salmon and energy production. The improved methods presented here should also reduce uncertainty in estimates of Chinook production based on RST monitoring data.

1.0 Introduction

With its dry climate, California rivers serve many important functions and there is not always enough water available for all. This study focuses on two important functions: reproductive habitat for salmon and hydropower generation. The San Joaquin Basin in the Central Valley represents a southern extreme of the distribution for fall-run Chinook salmon. Although fall Chinook salmon are not currently listed as threatened or endangered by the federal government, this species has been declining for many years in the San Joaquin Basin (Yoshiyama 2000). Wetter years are considered good for California's salmon because, among other things, higher flows in fall and spring lower water temperatures. One strategy that salmon biologists claim will help to recover Chinook salmon is to allocate higher flows during times of year when they are needed to ensure successful reproduction.

On the other side of this picture, the state of California has a significant need for hydropower. During the late 1990s, California experienced a sharp increase in energy prices and periodic rolling blackouts when the supply of energy failed to meet the state's demand. One of the causes of this crisis was drought conditions; others were regulatory. The energy deficits experienced by California highlight the importance of understanding whether or not legal restrictions on regulated flows to benefit salmon would result in a significant loss of energy capacity for the state.

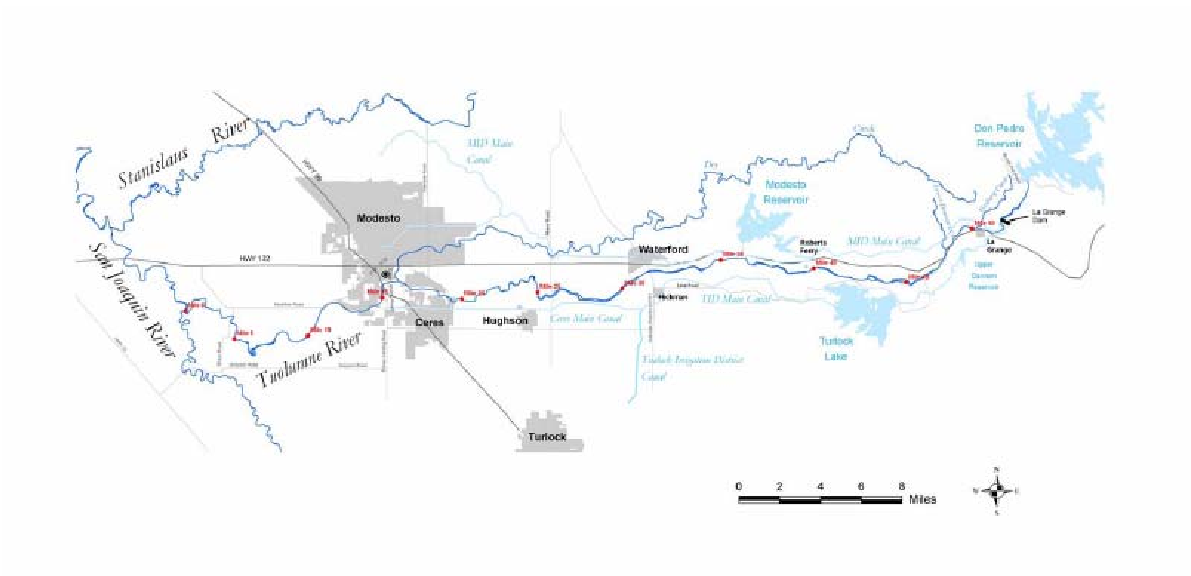
As part of a hydropower license for the New Don Pedro project, a 10-year study was instituted in the Tuolumne River to learn more about the influence of spring flows on Chinook production. Monitoring of outmigrating Chinook salmon was started around 1995, as a means of determining whether goals of increasing salmon production were being met. Rotary screw traps (RST)[1] were the primary monitoring devices used during the 10-year study. However, the traps do not operate every day, and daily totals must account for flow-related changes in capture efficiency. Therefore, one goal of this study was to improve field estimates of Chinook salmon outmigration, using statistical methods to impute estimates for missing days and to better account for flow effects on efficiency.

One promising way to quantify alternative strategies for allocating water is to use a model that can predict the effect of flow regimes on both salmon and hydropower. Several models, including the Oak Ridge Chinook Model (ORCM), have been developed to predict the effects of hydropower operations on salmon recruitment. Such models can help decision makers understand how decisions about seasonal and annual patterns in river flow will influence salmon production (Jager and Rose 2003). However, none of these models also predicts the effects of flow regulation on hydropower generation. A second goal of this project is to test and improve a quantitative tool for those making decisions about California's water, aquatic resources, and energy.

[1] A rotary screw trap (RST) is a floating device in which fish are trapped and held alive in a box for collection.

1.1. Fall Chinook Salmon in the Tuolumne River

Fall Chinook salmon spend their adult lives in the ocean. At some point between age 2 and 5, adults migrate into rivers during the fall to spawn. Each female digs a redd (nest) in the gravel river bottom. During courtship, she releases her eggs into her redd. She buries the eggs after they are fertilized by one or more males. Eggs incubate through the winter, hatch as alevins (non-feeding larvae) into inter-gravel spaces, and emerge from redds as fry (pre-smolt juveniles) in the spring. Fall Chinook salmon fry feed on invertebrates along river margins for the first month or two, and gradually move downstream. Fry may exit tributaries in winter or spring to rear in the lower main stem and estuaries prior to becoming smolts. During smoltification, juveniles become tolerant to saltwater and migrate to the ocean. This study focuses on the Tuolumne River, a tributary of the San Joaquin River (Figure 1). The LaGrange Dam, at 83.7 kilometers (km) above the confluence, blocks upstream migration of adult salmon returning to spawn. Flows are regulated by the much larger New Don Pedro Dam, just upstream.



Source: TID/MID 2005

Figure 1. Map of the Tuolumne River

1.2. Functional Validation

The predictive value of ecological models increases greatly when modeling is coordinated with long-term field studies. This is especially true when the field studies focus on measuring variables used by the model as input, or those that it predicts. An iterative process of confronting models with data leads to reduced uncertainty in model predictions (Hilborn and Mangel 1997).

The most common approach to model validation is to compare model predictions with field observations and to test goodness of fit between them at different times or places (e.g., Smith and Rose (1995)). One problem with using formal statistical tests to compare models and data is that a model with highly uncertain predictions can never be rejected. Another is that such tests rarely suggest directions for future improvement in either the data or model. Thus, Jager et al. (2000) suggested that statistical testing is a non-constructive approach to model-data comparison.

Functional comparison, to see whether model and data follow similar relationships with environmental variables, is more constructive because it reveals processes that are poorly represented in the model (or measured in the field) and it suggests areas of improvement in modeling or measurement. For example, this study used this approach to compare model predictions and field estimates of net primary productivity at the national (U.S.) scale. Results suggested that one of the models was exaggerating the response of net primary productivity to precipitation (Jager et al. 2000).

This report compares model predictions of Chinook salmon recruitment with those estimated from RST data in a California river. It initially focuses on two functional patterns that have already been described for juvenile Tuolumne River Chinook salmon: relationships with flow and density. The Turlock Irrigation District/Modesto Irrigation District (TID/MID 2005) concluded that the timing of downstream movements by fry, but not smolts, relate to flow. Earlier juveniles, called "fry," have not begun the transformation to tolerate saltwater, after which they are referred to as "smolts." Most juveniles captured in a low-flow year (2002) were captured after March, whereas most juveniles captured in higher flow years (1998 to 2001) were captured earlier, in February and March. TID/MID (2005) also reported a power relationship between fry density and spawner density the previous fall.

1.3. History of the Oak Ridge Chinook Model

The Oak Ridge Chinook Model uses an individual-based modeling approach to predict the influence of seasonal flow releases on fall and late-fall Chinook salmon recruitment in the Tuolumne River, California (see Attachment). Originally conceived as a tool for comparing alternative flow regimes proposed by stakeholders in the operation of New Don Pedro Dam (Jager et al. 1997), ORCM has been used to examine optimal patterns in seasonal flows from the perspective of Chinook salmon (Jager and Rose 2003). Both efforts yielded insights about the relationships between flow, temperature, and successful reproduction of the two salmon runs. Validation of some model predictions was possible; specifically growth patterns were compared against seining data. Growth predictions compared well with those observed in the field (Jager et al. 1997). Sensitivity analysis was used to identify critical variables for each of several model predictions (Jager et al. 1997). At that time, the primary response predicted by the model (the number of juvenile smolts outmigrating from the tributary) had not been measured in the field and, thus, could not be compared with model predictions. Since the initial model was developed, new monitoring data has become available.

In 1995, a settlement agreement was signed that modified the hydropower license for New Don Pedro Dam on the lower Tuolumne River. An adaptive monitoring program was implemented in 1996 that included monitoring of outmigrants for the period 1997–2004. Here, these data are used to compare functional responses to environmental variables with those followed by predictions of the ORCM.

2.0 Methods

Two goals of this project were: (1) to compare field and model results to reduce uncertainty in ORCM predictions, and improve RST estimates; and (2) to permit energy-salmon trade-offs to be quantified by adding the capability to estimate hydropower generation in ORCM.

Section 2.1 describes processing of field data and methods for ORCM model predictions. Section 2.2 describes methods for comparing the magnitude and timing of smolt outmigration predicted by the ORCM model and estimated from RST data. Subsequent sections describe methods to compare functional relationships between outmigrant counts and environmental variables, and methods for simulating hydropower generation.

2.1. Field Data

A research program monitors the production of fall Chinook smolts from the Tuolumne River (see TID/MID 2005). This program includes monitoring of outmigrating juveniles using rotary screw traps (Figure 2), which were installed in the Lower Tuolumne River by the California Department of Fish and Game (CDFG) in 1995 (TID/MID 2005). Two 8-foot diameter rotary-screw traps were operated in the lower Tuolumne River at the Grayson (river mile (RM) 5)/Shiloh Bridge (RM 3.5) locations to monitor the number, size, timing, and rate of fry and/or juvenile Chinook salmon emigrating from the Tuolumne River (TID/MID 2005). The sampling gear is stationary in the river current and operates in the upper part of the water column (TID/MID 2005). Each trap has an eight-foot diameter and capture any fish that swim downstream into the mouth of the trap. These traps operate on a subset of days, with a focus on what is believed to be the peak period of fall Chinook salmon outmigration in April and May. The number of juveniles captured is recorded for each time and date of operation, and the length is measured for a subset of individuals. Although measurements began in 1995, the first two years of data were too sparse to include. Only one trap was used in 1998.

Figure 2. Grayson rotary screw trap installed on the Lower Tuolumne River to sample outmigrating Chinook salmon

Only a fraction of salmon juveniles that are moving downstream are captured in the traps. To estimate the trap's capture efficiency, a known number of hatchery juveniles are released during field trials on dates with different flows. Trap efficiency is the ratio of the number captured to the number released. This ratio has been found to decrease with river flow. In addition, an adjustment is made for the proportion of the day when the trap is operated.

In summary, two adjustments are made to the data to obtain daily RST estimates. First, the number counted during a given day is divided by the proportion of the day sampled to get a daily total, N_d. Second, N_d is divided by trap efficiency, E_t, which depends on flow, Q_t in cubic feet per second (cfs) (Equation (1)).

$$E_t = a - b\,ln(Q_t) \tag{1}$$

Parameters a = 0.1464 and b = 0.0164 were fitted to data collected during field trials to assess trap efficiency (TID/MID 2005). The CDFG provided the research team with a spreadsheet, which calculated RST estimates for each day from flow.

Uncertainties associated with the RST estimates are high, because the trap efficiencies in the Tuolumne River are low. A minimum efficiency of 10% is sometimes cited as a lower limit for reliability. In the Tuolumne River, efficiencies are below this, even at moderate flows.

In the comparisons reported here, the research team improved estimation of efficiency at high flows, incorporated juveniles with imputed lengths, and separated RST juveniles smaller than and greater than 70 millimeters (mm). Each of these improvements is described below.

The research team accounted for the fact that the model predicts fry and smolts, where simulated juveniles become smolts when they reach 70 mm and have grown over a certain number of degree days (sum of degrees C). However, days with the highest counts included many juveniles that lacked length data. Because the team now required length information, it imputed lengths for juveniles lacking length measurements by determining the length frequency distribution for each day from measured individuals and applying these to the unmeasured counts to assign fractions of unmeasured juveniles to each length class.

One problem with the linear model in Equation (1) is that it can produce very small, and even negative, estimates of trap efficiency when flows are higher than those used to estimate the parameters. Very small efficiencies, when used in the denominator, produce very high RST estimates. In the first comparison, efficiencies at flows high enough to produce negative efficiencies were set to one, which likely underestimated counts on these dates. In the second round, the research team set efficiency estimates smaller than the minimum efficiency observed during the trial, which occurred at a flow of 6,400 cfs (181 cubic meters per second (cms)), to the observed minimum, E_{min} = 0.0027. An alternative solution would be to fit a logistic model rather than a linear one.

2.2. Model Predictions

The ORCM (Jager et al. 1997; see the Appendix) is a spatially explicit and individual-based model of fall chinook salmon recruitment in a river below a dam. The model links a spatially explicit representation of river habitat with a biotic model of chinook salmon reproduction, development, growth, and mortality. The river habitat changes seasonally and includes important spatial gradients (e.g., temperature, predator densities) between upstream spawning areas and lower reaches inhabited by juvenile salmon during outmigration. The biotic component uses a daily timestep to simulate coexisting life stages, as individuals grow, develop from one life stage to the next, move, and die. The ORCM simulates the river phase of chinook salmon ecology, beginning with adults entering the river to spawn. For each redd, the research team simulates the daily development and mortality of egg and alevin lifestages. After emerging from redds, the daily development, growth, mortality, and downstream movement of individual juveniles (fry and smolts) is simulated, culminating in the migration of smolts from the river (i.e., recruitment).

The biotic events leading from upmigration of spawners to the outmigration of recruits are simulated in a spatially explicit river habitat represented by a series of adjacent 1.6-km segments differing in the proportion of riffle and pool habitat, temperature, and flow (at confluences with tributaries or diversions). Simulated average daily water temperature in each river segment is determined by allowing water released by the dam (about 12°C year-round; FERC 1996) to equilibrate to the air temperature as the water travels downstream. The simulated river temperature of each segment depends on daily air temperature, dam release temperature, and flow rate, which controls the rate of travel downstream. Daily flow in each segment is generated as part of the optimization procedure and used to drive the ORCM.

The research team began by improving the simulation of downstream variation in water temperature in the Tuolumne River using available data. The ORCM model requires daily average flow and temperature data (water and air), and predicted downstream water temperatures daily. The team obtained temperature and flow data for a variety of locations in the Lower Tuolumne, using United States Geological Survey (USGS) daily data when and where available, but supplemented with averages calculated from hourly temperature data and recent data obtained from the California Data Exchange Center,[2] which is maintained by the California Department of Water Resources. The research team obtained recent, but incomplete, temperature data at a larger number of sites on the river. These data were used to calibrate a simpler model for spatial variation in temperature. Researchers compared the fit of a variety of linear and non-linear regression models used to predict longitudinal temperatures (°C) at all downstream locations (T_x) from release temperature at LaGrange Dam (T_r), air temperature (T_a), distance downstream in km (x), and release flow in cubic meters per second (m^3s^{-1}) (Q). Equation (2) fit the best and replaced the original equation in ORCM.

[2] http://cdec.water.ca.gov/

$$T_x = b_0 + T_r + b_1(T_{air} - T_r)\left(1 - e^{-b_2 x Q^{b_3}}\right) \tag{2}$$

Ideally, model validation is an iterative process in which feedback from comparison with field data leads to improvements in the calibration or structure of a model. Here, the research team completed two rounds of model-data comparison and iterated the process of making model predictions and comparing them to data. The two versions of the model are referred to as *ORCM-I* and *ORCM-II.* The study's first objective was to adjust the average number of outmigrants predicted by ORCM to match field estimates. The research team started by using the same parameter values used in previous simulations (see the Attachment). The team determined that ORCM outmigrant numbers tended to be higher, and next, tried to determine during what lifestage survival was higher in the model than in the field. ORCM predictions of egg-to-fry survival in Round I were higher (average = 0.57; range: 0.21 to 0.79) than field estimates of survival to emergence and an empirical model based on gravel permeability, which varied from 0.34 to 0.51 (TID/MID 2005). Although other parameters influence egg-to-fry survival, the research team had no reason to modify mechanistic factors, and therefore focused on baseline egg mortality as the parameter to calibrate. For Round II, the team increased baseline egg mortality, *eggm* = 0.012, to match the observed mortality. The team also observed that juvenile survival was higher. Juvenile survival in the model is influenced by predation, temperature, and premature emigration. The authors are confident in the study's simulation of temperature-related mortality, and to a lesser extent in estimates of premature migration, but less so in predation rates. In addition, changes in the river have altered the density of warmwater predators (bass) and spatial overlap between predators and Chinook salmon juveniles (TID/MID 2005). The research team therefore increased the probability of capture for predators, *pcap* = 0.001 from 0.0001 using the simplified predation model (see the Attachment). The equations in which these parameters are used are given in the Attachment. In the second round, the research team also modified ORCM to reading in the proportion of female spawners in each year rather than using the same sex ratio for all years. By doing this, the team hoped to refine the predicted timing of outmigration.

2.3. Comparison of Outmigration Magnitude and Timing

The research team graphed the number of outmigrants on each day between the beginning of March and early June. Different graphs are presented for each year and for each of the two rounds. All sizes of juveniles, both fry and smolts, are included in these graphs.

2.4. Functional Comparison

Differences between the relationships observed in field data and model-predictions can provide guidance in further improving processes in the ORCM model. This approach was successfully used to evaluate three regional models for net primary productivity (Jager et al. 2000), and discovered that one model was over-responding to precipitation. Here, we developed empirical relationships to describe the daily number of outmigrating smolts for both the RST data and the ORCM predictions. We contrasted the coefficients of relationships between smolt numbers and key predictors, including degree-days, escapement (i.e., number of spawners counted the previous fall), and flows.

The research team fitted daily smolt numbers as a function of predictors that changed within and among years for the seven years between 1997 and 2004. R software[3] was used for the statistical analyses reported here. The team fitted one set of models to all the data, keeping zero smolt counts (days when the traps were operating but caught no salmon), and another set of models to the subset of days with non-zero smolt counts. The team added the analysis with only non-zero counts, in part, to help satisfy distributional assumptions. Interpretation of these models is also slightly different: the set of models fitted to days with non-zero smolt counts predicts abundance, given that migration is occurring.

The annual production of saltwater-tolerant smolts that leave the river to migrate seaward depends on the number of spawners or "escapes," *Esc*, the previous fall. The research team expects more smolts to be produced when there are more spawners to product them up to a point. Beyond a certain number of spawners, "density dependent" factors cause the number of offspring that survive to migrate downstream as smolts to reach a limit or even to decrease. Examples of density-dependent mortality exist at all stages. Beginning with reproduction, adults may interfere with one another during spawning. Adults that arrive on the spawning grounds later might dig their nests (redds) for their eggs right on top of those of previous spawners, which causes mortality of the earlier eggs. This is called "superimposition" of redds. After hatching, larvae (called "alevins") reside in the interstices of the gravel riverbed. High alevin densities can reduce water quality by depleting dissolved oxygen and high levels of ammonia (waste products). After emerging from the gravels, juveniles (both fry and smolts) are exposed to predation. At high densities, smaller, later-emerging fry have trouble competing for feeding territories. Consequently, more fry remain small and vulnerable to predation when densities are high.[4] The Ricker function (below) is one function that is typically used to represent this dependence on spawner density. Equation (3) below shows a general or extended form that includes other, potentially time-varying, environmental predictors, in linear function, $f_t(.)$, for calculating daily smolt outmigrants, $Y_{i,t}$ for each year i and day t.

$$Y_{i,t} = Esc_i \cdot e^{b_0 + b_1 Esc_i + f_t(.) + \varepsilon} \qquad (3)$$

The research team linearized Equation (3), as shown in Equation (4), to obtain parameter estimates and to examine the evidence for density dependence in daily smolt outmigrants, $Y_{i,t}$, where smolt counts are daily (indicated by subscript t) and the number of escapes is the same within a year (indicated by subscript i). To avoid taking the log of zero on days when

[3] The R Project for Statistical Computing. www.r-project.org/.

[4] However, at high juvenile densities, predators become saturated and are unable to eat as large a fraction of available fry and smolts—an example of inverse density dependence.

no smolts were observed and/or predicted, the research team added a one to the number of smolts in datasets that included zero counts. The error term, ε, is assumed normally distributed with zero mean and variance-covariance matrix ∑ for the linearized equation below.

$$\log_e\left(\frac{Y_{i,t}}{Esc_i}\right) = b_0 + b_1 Esc_i + f_t(\bullet) + \varepsilon, \quad \varepsilon \cap \mathbb{N}(\vec{0},\Sigma) \tag{4}$$

The research team evaluated the residuals of the models for the RST data to determine the extent to which they followed an independent (i.e., no autocorrelation) normal distribution with zero mean and a constant variance, which is assumed by linear regression. For residuals with no autocorrelation, the expected correlation between two values separated by one day would be the same as the expected correlation between two values separated by one hundred days, which in both cases would be zero.

Analysis of the residuals indicated strong autocorrelation in the residuals of the models examined. The research team therefore used generalized least squares to fit the Ricker models described below. Generalized least squares allowed us to model and incorporate the autocorrelation structure. The team used the exponential covariance model shown in Equation (5) to model an exponential decay in autocorrelation over time. According to this model, the expected correlation between pairs of residuals is smaller when they are more days apart. Equation (5) was fitted to the residuals and used to construct the appropriate variance-covariance matrix, Σ, and solve for the parameters of Equation (4). The final estimate of λ in Equation (5) is reported. The same procedure was used to solve each of the extended Ricker equations to be described later.

$$C(\Delta t) = e^{-\lambda \Delta t} \tag{5}$$

The following information is presented for each model:

- A Pearson correlation between predictions of outmigrating smolts,[5] Y_t, and either RST or ORCM-II predictions. Squaring this value estimates the percent explained variance.
- Akaike's information criteria[6] (AIC) to compare models and the residual standard error.

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[5] Note that these are estimates of median outmigration, back-transformed from the log-transformed ratios predicted by Equation 4. The mean can be estimated by adding half the estimated error variance to the linear equation before taking its exponent and dividing by Esc_i.

[6] Akaike's information criterion (AIC) is an index that penalizes for the number of predictors included in a model (Akaike 1974). In contrast, the R^2 always increases as more predictors are added.

- Estimated coefficients, and the probabilities associated with the T- test of a two-sided hypothesis that each is zero.
- The estimated range of the exponential variogram model.

The research team expanded the function, *f*, in Equation (4) to include predictor variables that represent within- and among-year variation in smolt counts. The team hypothesized that within-year variation in smolt counts (i.e., timing) is related to the cumulative temperature (degree days) since the beginning of the current year, $DD_{i,t}$, and $DD_{i,t}^2$, as shown in Equation (6). Degree days reflect the physiological time that juveniles have to develop into smolts, which is largely controlled by temperature.

$$\log_e\left(\frac{Y_{i,t}+1}{Esc_i}\right) = b_0 + b_1 Esc_i + b_2 DD_{i,t} + b_3 DD_{i,t}^{\ 2} + \varepsilon \tag{6}$$

In addition to temperature and escapement, flow could also explain variation in smolt production. The research team considered a variety of models involving lagged flows, with lags between 5 and 21 days. However, the team focused mainly on the following flow variables, which have one value for each year, *i*:

1. *Qfall* - fall flow (that from the previous October or November).
2. *Qwinter* - winter flow (December to February).
3. *Qspring* - spring flow (March to June).
4. *Qcum* - cumulative flow between February 15 of the current year and the date of outmigration.
5. *Qsd* - standard deviation in flow between February 15 and the date of outmigration.

$$\begin{aligned}\log_e\left(\frac{Y_{i,t}+1}{Esc_i}\right) &= b_0 + b_1 Esc_i + b_2 DD_{i,t} + b_3 DD_{i,t}^{\ 2} \\ &\quad + b_4 Q_{fall,i} + b_5 Q_{winter,i} + b_6 Q_{spring,i} + b_7 Q_{cum,i} + b_8 Q_{sd,i} + \varepsilon\end{aligned} \tag{7}$$

The research team considered models with flow at all lags up to 21 days (but no other flow variables) and one lag at a time. The dynamic linear modeling package, available in the R software, was used for time-series regression analysis of models involving temporally lagged flows. These lagged-flow models were not predictive and results are not shown here. In the model with all lags, the team found only one or two lags to be significant, with little overall predictive power. The particular lags that were significant depended highly on which other lags were included, suggesting high autocorrelation in flow. Considered individually, flow lagged by 10 days was the most significant when added to Equation (6) for the RST data (zero counts included).

The research team identified a different "best" model for the RST data by removing predictors from Equation (7) that were not significant and examining correlations among parameter estimates. The team favored models with the lowest AIC. The model in Equation (8) was selected for RST data with dates having zero counts removed.

$$\log_e\left(\frac{Y_{i,t}}{Esc_i}\right) = b_0 + b_1 DD_{i,t} + b_2 DD_{i,t}^{\ 2} + b_3 Q_{spring,i} + b_4\left(\sum Q_t\right)_i + b_5\left(\sum Q_{sd}\right)_i + \varepsilon \qquad (8)$$

This study's functional validation compares the fitted models for RST data to the corresponding models for ORCM predictions. The research team's goal is to identify differences in coefficients that reflect differences in environmental responses of model-predicted and field-estimated smolt numbers.

2.5. Imputing RST Estimates

The date of peak outmigration clearly changes from year to year, and appears to be driven by temperature-related development of smolts more than by flow and other environmental variables. Predicting this more precisely might be useful for tailoring the dates of pulse flow releases, which are costly in terms of foregone energy production. The significant degree-day relationship in Equation (4) can be used to find the degree days (DD) when outmigration is at a peak by calculating the derivative of Y with respect to DD for coefficients for the RST data. The derivative was set to zero, and solved for $DD^* = -b_2 / (2\ b_3)$, which holds for the general case also (i.e., where the Escapement term is replaced by $f(\cdot)$). For demonstration purposes, the research team estimated DD* using coefficients from Equation (6) fitted to RST data excluding zero counts.

In addition, any of the empirical relationships could be used to impute smolt counts for days when the rotary screw traps were not operating. The research team obtained imputed totals using Equation (6) fitted to RST data excluding zero counts. Imputed values obtained in this manner were used to obtain annual totals, but not for functional validation.

2.6. Energy Generation

The research team's final task was to add the capability to estimate hydropower generation in ORCM, making it possible to evaluate tradeoffs between hydropower generation and salmon production. The team combined annual flow data for the Tuolumne River below LaGrange Dam (USGS gage 11289650) with annual generation data from the U.S. Department of Energy's EIA-860 database (generator id's pcode = 439 and 440 for LaGrange and the New Don Pedro). A linear relationship between river flow and electricity generation is suitable for dams that produce electricity with a fixed hydraulic head (Kotchen 2006). The research team fitted a linear model to explain annual generation as a function of total annual river flow. The coefficients were then input to the ORCM model and used to estimate daily generation from daily flows.

3.0 Results

3.1. Comparison of Outmigration Magnitude and Timing

ORCM predictions in Round I were much higher than RST estimates of smolt outmigration for all years. After reducing egg survival and increasing predation on fry, ORCM-II predictions were closer to RST estimates for three years—1998, 1999, and 2004—but the totals for 2000–2003 remain much higher (Figure 3). RST estimates suggest fewer than 10 smolts emigrated per spawner in all years, whereas the model predicted a much more variable number of smolts per spawner, from 1 to 62 (Figure 3). Spawner abundance measured in the Tuolumne River was highest in the fall of 2000 (17,873), lowest in 2003 (2,961) and similar in other years (7,125–9,222) (TID/MID 2005).

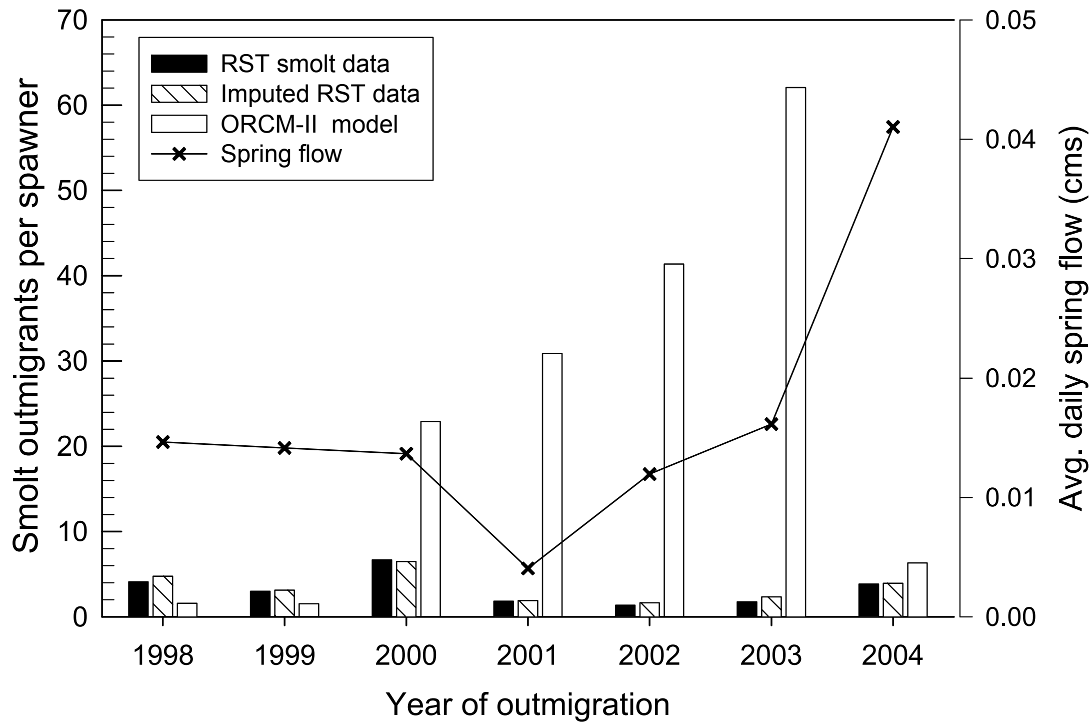

Figure 3. Comparison of total smolt outmigrants (bars) predicted by ORCM in rounds I and II and those estimated from RST data during the spring of 1998 to 2004. The line depicts average spring flow.

The simulated peak date of smolt outmigration compared well (within a week) with RST data for four of the seven years (the spring of 1998 and 2002–2004). During the period 1999–2001, predicted average outmigration date differed by up to 17 days, with no clear bias earlier or later. The average outmigration julian date, weighted by numbers of smolts, are shown in Table 1, and include all ORCM predictions. Statistics in Table 1 include ORCM predictions for all dates. ORCM-II predicted outmigration peaked earlier than RST in the spring of 1999 and 2000, later in 2001, and during a similar timeframe in the later years. Timing did not change much between the two rounds of validation, except for the spring of 2000.

Table 1. Average julian date of smolt outmigration for RST data and ORCM-II predictions, which included all dates (not just those with RST data)

Year of spring	Rotary screw trap data	ORCM-II predicted	Difference (d)
1998	103	106	3
1999	115	101	-14
2000	112	96	-16
2001	108	125	17
2002	116	116	0
2003	115	110	-5
2004	110	116	6

3.1.1. Functional Comparisons

This section compares results for the non-flow model (Table 2). Next, it compares results for a "complete" model that includes flow variables (Table 3). Finally, it shows parameters for the "best" model for RST data, as determined by AIC and examination of correlations among the predictors.

3.1.2. Functional Responses to Degree Days and Escapement

Functional relationships produced by the ORCM-II model and RST data showed similarities and differences. The regression analysis of RST data and ORCM-II predictions using Equation (6) showed several similarities. Both model and field data showed a significant quadratic (parabolic) response to degree-days when zero counts were included (Table 2). Degree days (cumulative temperature) are an important predictor, presumably because of its ability to predict the onset of smolt outmigration and daily variation in smolt outmigration (timing).

Autocorrelation was also a persistent feature of both field estimates and model predictions of outmigration, and residuals of regression models to predict outmigration. However, the range of the exponential correlation function, which measures the length of time within which residual errors are autocorrelated, error differed, with autocorrelation over a shorter range for RST data than for ORCM-II predictions (1.4 and 15.5 days, respectively).

An important feature of the Ricker model is its ability to represent density-dependent effects, i.e., a decrease in smolt production at high spawner densities due to superimposition of redds and other mortality risks that increase with density. The research team considers density dependence to be significant when the coefficient b_3 (Table 2) is significantly less than zero ($p \leq 0.05$). RST and ORCM-II showed different responses to spawner density (Table 2). When fitted to Equation (6), the "Escapement" coefficient fitted to the RST data showed the expected negative sign, whereas this term had a positive sign model for ORCM-II predictions. This indicates a decrease in RST outmigrants at high spawner densities, but a stronger-than-linear positive response to escapement in ORCM-II predictions over the range of densities simulated.

Table 2. Comparison of empirical regression models for $\log_e$(smolts / escapement) shown in Equation (6) for RST-estimated and model-predicted smolt outmigrants in the lower Tuolumne River with and without zero counts included

Coefficient	Variable	RST (zeroes included)	$P<\vert T\vert$	RST (zeroes excluded)	$P<\vert T\vert$	ORCM-II (zeroes included)	$P<\vert T\vert$	ORCM-II (zeroes excluded)	$P<\vert T\vert$
b_0	Intercept	-12.7922	0.0000	-5.7428	0.0000	-7.0344	0.0000	-2.9171	0.3712
b_1	DD	0.01250	0.0002	0.00550	0.0002	0.00325	0.0332	0.00066	0.8845
b_2	DD^2	-0.000004	0.0001	-0.000002	0.0001	-0.000001	0.0342	0.0000004	0.8081
b_3	Escapement	-0.000013	0.7285	-0.00010	0.0123	-0.00011	0.2765	0.000027	0.7309
	Correlation	0.2286		0.2287		0.2217		0.5466	
	Residual SE	1.1308		1.1308		3.209		1.8171	
	Residual df	542		388		1102		312	
	AIC	2114.0		1075.43		3385.25		896.02	
	Range (d)	1.1		2.2		16.5		7.1	

DD = degree days; Residual SE = residual standard error; Residual df = residual degrees of freedom; Range (d) = range parameter value of the exponential autocorrelation function; $P<|T|$ = probability of a T-statistic < the absolute value of T.

Table 3. Comparison of the full empirical regression models for $\log_e$(smolts / escapement) shown in Equation (7) for RST-estimated and model-predicted smolt outmigrants in the lower Tuolumne River with and without zero counts included

Coefficient	Variable	RST (zeroes included)	P<|T|	RST (zeroes excluded)	P<|T|	ORCM-II (zeroes included)	P<|T|	ORCM-II (zeroes excluded)	P<|T|
b_0	Intercept	-16.491	0.0000	-8.8638	0.0000	-15.1496	0.0000	-6.9706	0.2804
b_1	DD	0.0178	0.0000	0.00724	0.0000	0.01714	0.0001	0.00789	0.2817
b_2	DD^2	-0.0000006	0.0000	-0.000002	0.0001	-0.000006	0.0000	-0.000002	0.3259
b_3	Escapement	0.0000017	0.8644	-0.000027	0.7411	0.000030	0.8609	0.000464	0.0011
b_4	Fall flow	0.000082	0.9390	0.000376	0.6633	-0.001114	0.6350	-0.00592	0.0010
b_5	Winter flow	-0.000023	0.4218	-0.000026	0.3165	-0.000244	0.7206	-0.000643	0.2454
b_6	Spring flow	0.000077	0.1741	0.000190	0.0001	-0.000033	0.9000	0.000166	0.3187
b_7	Cum. flow	-0.000112	0.4755	-0.000329	0.0071	-0.000312	0.4280	-0.000341	0.5447
b_8	SD flow	0.00452	0.8501	0.01507	0.4610	0.07642	0.1721	0.16636	0.0014
	Correlation	0.2363		0.3414		0.6785		0.7672	
	Residual SE	1.737		1.0657		3.1815		1.3237	
	Residual df	436		380		669		301	
	AIC	1849.33		1135.76		2424.0		926.31	
	Range (d)	0.9		1.9		10.7		3.6	

SD flow = standard deviation in flow.

3.1.3. Functional Responses to Flow Variables

Next, the research team examined Equation (7), which included a set of summary flow variables in addition to degree days and escapement. These models cannot be compared with those in Table 2 using AIC because a subset of days are dropped when variables "Cum flow" and "SD flow" are added.

In the models with zero counts included, none of the flow variables was significant for either the RST data or ORCM-II predictions (Table 3). In models fitted to data with zero counts excluded, a few flow variables became significant, suggesting that flow variables influence the number migrating on a given day, but not whether or not migration occurred. Equation (7) includes some predictors that are significant for one and not the other (RST versus ORCM-II). These differences are the focus of this study's validation. Spring flow and cumulative spring flow were significant predictors for RST outmigrants, but not for ORCM-II (Table 3). Fall flow and the standard deviation in flow since February 15 (SD flow) were significant predictors for ORCM-II, but not for RST outmigrants (Table 3). Finally, it is noted that escapement, which played a significant role in Equation (6), was not important in the full models that included flow variables (Table 3). This suggests that the effects of escapement were correlated with, and replaced by, other predictors (e.g., the correlation between parameter estimates for escapement and fall flow was -0.764).

The "best" RST model included degree-days, spring flow (total and cumulative), and variation in flow (Table 4). Note that the three flow variables do not greatly increase the predictive capability, as measured by the correlation, over that in the model with just degree days and escapement (Table 2).

Table 4. "Best" empirical regression models for loge(smolts / escapement) shown in Equation (8) for RST-estimated smolt outmigrants in the lower Tuolumne River (zero counts excluded)

Coefficient	Variable	RST	P<|T|
b_0	Intercept	-8.2961	0.0000
b_1	DD	0.006633	0.0001
b_2	DD^2	-0.000002	0.0002
b_4	Spring flow	0.000173	0.0000
b_5	Cum. flow	-0.000267	0.0033
b_7	SD flow	0.013277	0.1263
	Correlation	0.3079	
	Residual SE	1.038	
	Residual df	380	
	AIC	1081.54	
	Range (d)	1.9	

3.2. Imputing RST Estimates

First, the research team proposes that the correction for catchability as a function of flow can be improved by using the maximum flow that occurred during efficiency tests. In addition, there is some question about the Modesto flow data, which are quite a bit higher than those provided by USGS. The team applied the first correction (but not the second) before running these analyses. Second, the team estimated the degree days at peak outmigration from fitted parameters for RST data as 1,563 degree days by solving for the optimal value in Equation (6) with coefficients derived from RST data with zeroes included (Table 2). Third, the team used one of the models developed as part of this study's validation, a Ricker model involving previous-fall escapement and degree-days, to impute rotary screw trap estimates for missing days (Figure 4). Using the same model as above, the team estimated the following annual totals: 5,244 in 1997; 35,510 in 1998; 27,954 in 1999; 51,025 in 2000; 36,253 in 2001; 14,695 in 2002; and 15,264 in 2003.

3.3. Energy Generation

The linear relationship, Generation (MWh) = 295,807 + 7814.1 Flow (cms) explained 77% of variation in annual generation at the New Don Pedro and La Grange projects between 1970 and 2003. The research team incorporated this relationship in ORCM to allow simultaneous prediction of salmon production and hydropower generation. To scale from annual to daily flows, the team divided the intercept by 365 days. For linear relationships such as the one above, disaggregation does not introduce error (O'Neill 1979). Figure 5 shows the relationship between flow and generation over the period of study.

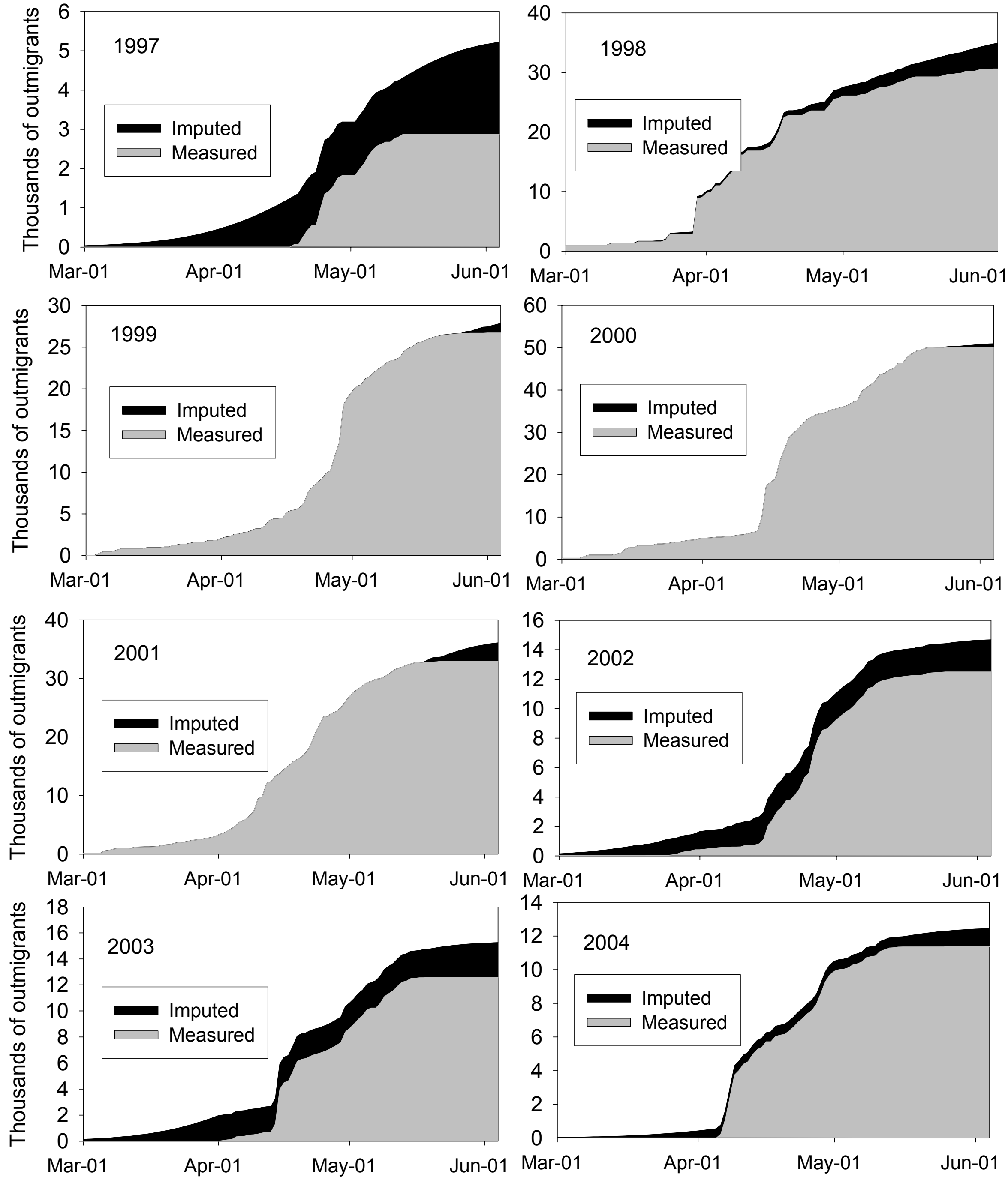

Figure 4. Cumulative estimates of outmigrants > 70 mm in size based on rotary screw trap data collected by the California Department of Fish and Game. The black shaded area shows the additional estimated Chinook smolt production using the imputation method described here, and the grey shaded area shows the cumulative production without imputing missing dates.

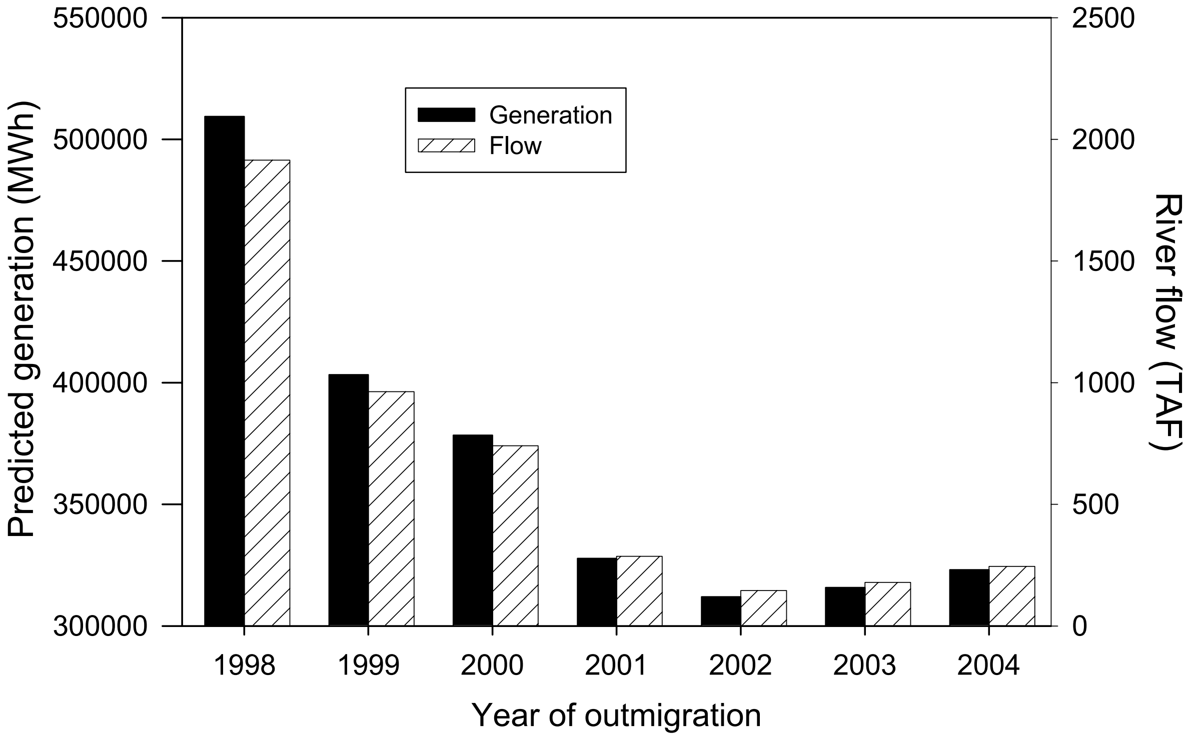

Figure 5. Relationship between ORCM-simulated generation and cumulative river flow over the 330 days simulated by the model in each year

4.0 Discussion

Three objectives of this study were: (1) to improve RST estimates of outmigrating juveniles, (2) to reduce uncertainty in ORCM predictions, and (3) to add the capability to estimate hydropower generation in ORCM, which will allow both energy production and salmon production associated with a given flow regime to be predicted.

This study's first objective was to reduce uncertainty in RST estimates of annual numbers of outmigrants. The empirical relationships presented earlier as part of the functional validation were useful for pursuing this objective. First, the research team used one relationship to solve for the degree-days at peak smolt outmigration, which could be used to fine-tune the timing of pulse flows. Second, the team used one relationship to impute outmigrant counts on dates when the rotary screw traps did not operate. In practice, these relationships should first be verified using cross-validation against new data not previously used to estimate parameters.

This study's second objective was to reduce uncertainty in ORCM predictions. Because the research team only completed two rounds of model comparison, this objective was not fully accomplished. However, the team made a start and developed methods needed to continue the effort. Discrepancies between model-predicted survival and that suggested by field sampling remain unacceptably large for some years. This study's comparison of timing of outmigration showed differences in some years, but not others. Because ORCM uses the same temporal distribution of spawners in fall of each year, timing of outmigration in the model does not reflect year-to-year differences that are likely to be observed in the field.

The consequences of extreme weather events and density dependent mortality are two possible reasons for the discrepancy between the model and data. This study's functional analysis suggests that density dependent mortality is higher in the field than simulated in the model. Another line of evidence suggesting that the "missing" mortality must be density dependent is that increased density-independent mortality would result in no smolt outmigrants in the three years now predicted reasonably well: 1998, 1999, and 2004. Two sources of density-dependent mortality that are now simulated by ORCM are redd superimposition and predation on fry. However, the parameters controlling the strength of each of these density dependent factors may need tuning.

It is difficult to say from the RST data whether the additional, unpredicted mortality occurs during the egg or fry life stage. The RST data are not useful for addressing this question because fry outmigration was not sampled in most years. The most complete early sampling occurred in 2000 and 2002. During these two years, ORCM-II predicted 5-times (in 2000) and 100-times (in 2002) more fry outmigrants than were estimated based on the rotary screw trap data. Thus, higher egg and alevin mortality may have occurred during these two years than the average value estimated in the field and used by us as input to the model. Increasing egg mortality in the model to correspond to those in field tests was not sufficient to produce such low numbers (simulated egg-to-fry survival ranged from 0.06 to 0.20).

Juveniles in the Tuolumne River might grow slower at high densities, and thus risk higher exposure to predation for a longer period. To test the hypothesis that density-dependent mortality is caused by slower growth, growth rates in the different years could be compared, to see whether there is evidence in the RST and seining data of slower growth at high densities, and whether density-related differences in growth are tracked by growths simulated in ORCM. Preliminary comparison of an annual growth index and seined juvenile densities do not suggest an inverse relationship (TID/MID 2005; also Figure 6).

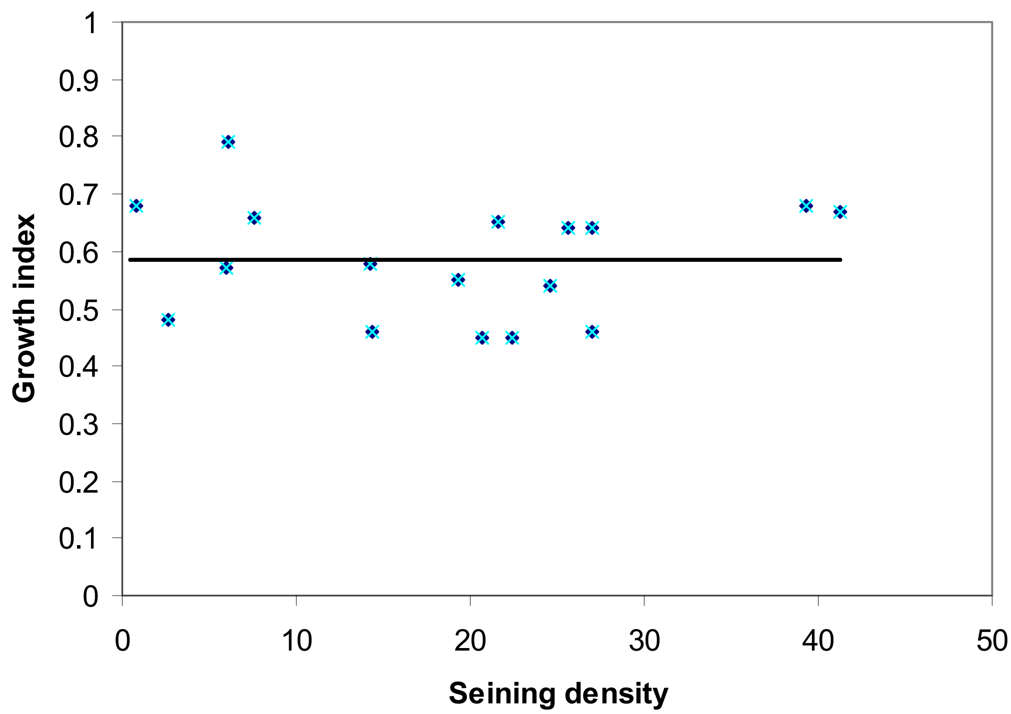

Figure 6. Juvenile growth index (mm/d) showed no relationship with seining density

Another possibility is redd superimposition, which is known to occur in this river (TID/MID 2005). To address superimposition, we could consider whether the spatial distribution of spawners is more concentrated near the upstream dam, leading to higher levels of superimposition than is currently simulated in ORCM.

If the research team were to continue the process of iterative improvement, identifying density-dependent influences would be the next focus. The most powerful test of density dependence requires approximately 16 years of population estimates (Dennis and Taper 1994).

Flow influences salmon directly through velocity and depth (i.e., physical habitat), and indirectly, through temperature—water released by the dam is, in general, colder than air in fall and spring and warmer than air in winter. This study's results suggest that temperature-related effects of flow are more important than the direct effects of flow as predictors of outmigration time. Neither model nor data showed a large increase in predictability after including flow variables, none of which were significant in models fitted to data including zero counts. However, patterns in the models fitted to data excluding zero counts suggest that flow variables correlate better with overall abundance than with timing. In these data, the research team did observe differences between the RST estimates and model predictions: ORCM-II predictions showed a weaker response to spring flow and cumulative spring flow, and a stronger response to fall flow and variation in spring flow, than was observed in the RST data. In a next round of model validation, these differences might be examined for clues to model improvement. In addition, there is always the possibility that observed effects of spring flow on RST data reflect the effects of correcting RST counts for low efficiency at high flow. In future efforts, it would be instructive to include an index of maximum temperature as an additional predictor to determine whether ORCM predictions of temperature-related mortality are sufficiently accurate.

Analysis of residuals revealed that the episodic nature of outmigration, combined with the presence of many small (and zero) counts, makes prediction difficult. One would think that a hierarchical model including a logistic function for the presence-absence of outmigrants and a separate model to predict counts, given the presence of outmigrants, would improve prediction, but this was not found to be the case in this study's preliminary assessment. Even residuals of the "best" linearized equation for RST data show the difficulty of predicting many small counts and few large counts using the predictors available (Figure 7). This suggests that the extended Ricker model does not represent the error structure of these data particularly well. Others have encountered the same problem in dealing with Chinook migration data (e.g., Zabel et al. 2005).

Several studies have quantified relationships between Chinook salmon migration rate and river conditions, such as flow, temperature, and turbidity (Connor et al. 2003; Smith et al. 2003). However, the research team identified only one other study that attempted to predict the numbers migrating at different times (i.e., timing of migration). Trepanier et al. (1996) developed a time-series model to predict the upstream migration of landlocked Atlantic salmon as a function of river discharge and water temperature. The authors argued for a need to include autocorrelation in prediction and demonstrated the facts that model significance and the significance of individual predictors are overestimated by ordinary least squares models that assume residuals are uncorrelated.

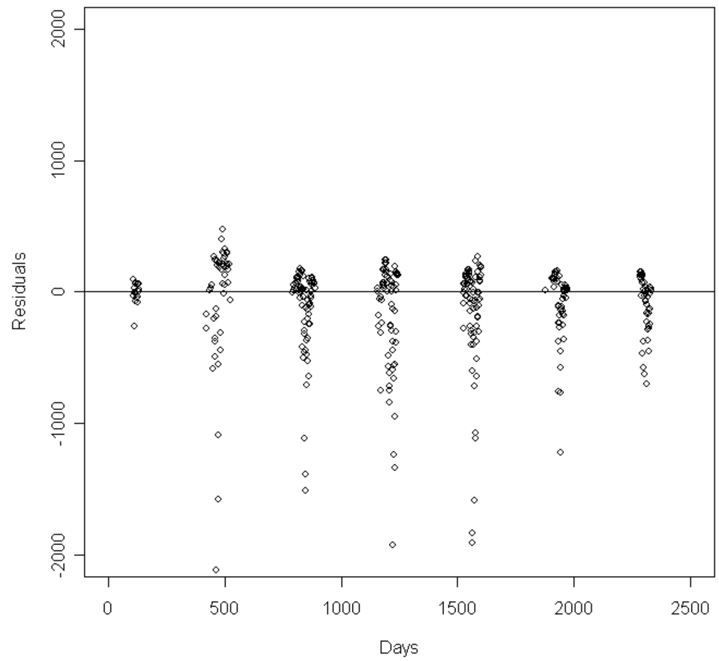

Figure 7. Residuals from the model shown in Equation (8) for $\log_e$(RST-estimated smolt outmigrants/Escapement) over time (1997–2004)

The residuals in the present study also showed considerable autocorrelation: Figure 8 shows the average correlation between pairs of values separated by the number of days on the x-axis. The research team was able to account for autocorrelation in the analysis by using generalized least squares. This study's analyses of time series models with lagged variables suggested that models including earlier counts could substantially improve predictions and, consequently, whiten (i.e., reduce autocorrelation among) the residuals. In the authors' opinions, it is unlikely that such feedback could be provided quickly enough to be useful in practice, and model-data differences in autocorrelation would not be easy to interpret for purposes of functional validation.

This study's third objective was to calculate energy production in the ORCM model. The research team met this objective by developing an equation that predicts energy generation from flow based on historical data from the USGS and the U.S. Department of Energy's Energy Information Administration (EIA). This equation was incorporated into the ORCM model and will make it possible to quantify the flow-related trade-offs between salmon production and energy production. Flow-based predictions of generation could be refined by incorporating reservoir elevation, which determines the "head" (i.e., the vertical distance between the water surface and the turbines). The relationship presented here predicts well on an annual basis, and the authors are confident that distributing the energy generation across days based on flow results in accurate predictions.

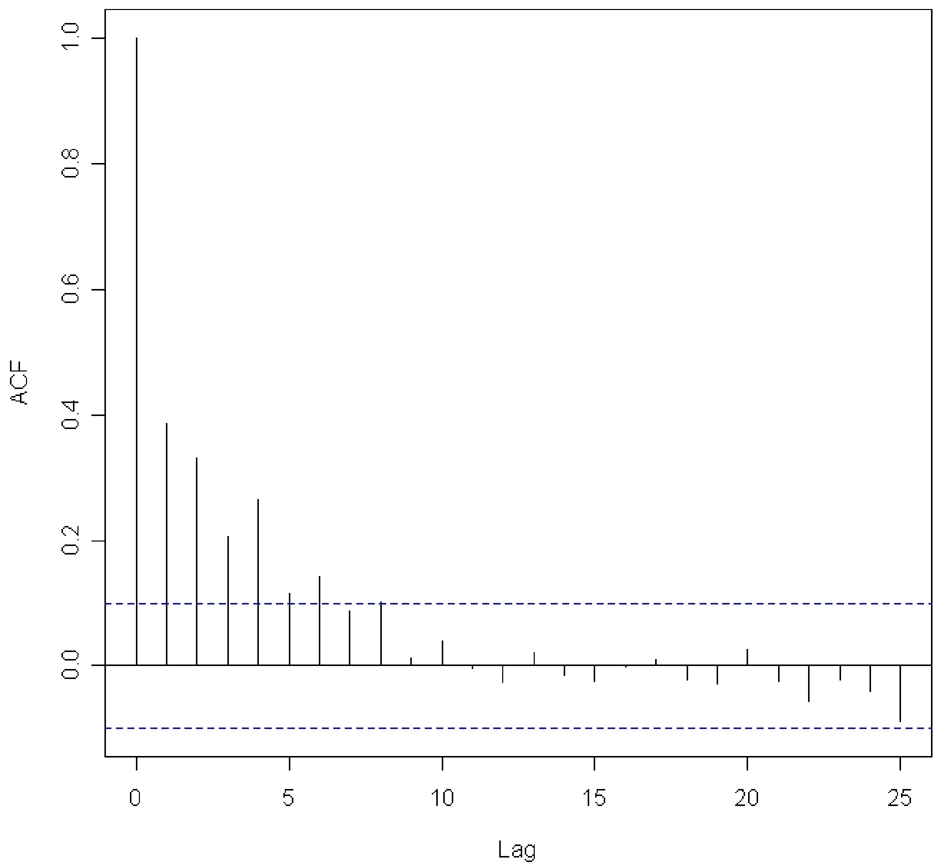

Figure 8. Temporal autocorrelation in residuals from the model given by Equation (8) for RST data excluding zero counts. The x-axis shows the lag in days and the y-axis shows the autocorrelation function, ACF.

The research team did not attempt to estimate the value of hydropower generation. Stewart (1997) estimated that each acre-foot of water diverted through turbines in the Sierra-Nevada region of California produces $15 of electric power valued at a wholesale power rate of 2.5 cents/kilowatthour (kWh). It would be difficult to incorporate such a fixed conversion because of the temporal variation in markets and demand-driven variation in price. Hydropower is typically of higher value during hours of peak demand (daytime) to offset the cost of buying power from fossil fuels or other sources. In future, seasonal variation in price could be incorporated to estimate hydropower revenue.

5.0 Conclusions

The approach used by this study will eventually reduce uncertainty in model predictions and field estimates by improving understanding of model-data discrepancies. Both the model and data involved in this study are characterized by high uncertainty. Low capture probabilities increase the uncertainty in RST-based estimates, which are obtained by statistically cloning one captured fish to represent hundreds that were not caught. This makes it difficult to know with confidence how many outmigrants exited the river in a given year. On the model side, ORCM predictions vary considerably from year to year, a phenomenon not observed in the RST estimates. Because only two rounds of comparisons were completed, this study has reached the stage of highlighting uncertainties in model predictions, while somewhat reducing uncertainty in RST estimates.

As one result of this study, the research team provided guidance for the next steps in iterative model improvement. Two hypotheses that may explain why observed survival in the field was lower than predicted in half the years are (1) under-representation of density-dependent mortality in the model, and (2) fish kills due to factors not represented, or not adequately represented, in the model (e.g., episodes of low dissolved oxygen, high temperature, or contaminants). The first hypothesis can be tested using other sources of information—in particular seining survey data. Average sizes of salmon in the seining data should indicate when migration is likely to occur, and the relationship between fry and smolt abundance in the river and the number of outmigrating smolts captured in RST traps. A decoupling between these two could indicate a high, density-dependent mortality acting on fry, whereas a strong positive relationship between fry and smolts, combined with a weak relationship with spawner abundance, would suggest that density-dependent mortality during the egg stage is important. One could begin to examine the second hypothesis by adding maximum temperature over some previous time interval as a predictor in the functional comparison. Although temperature-related mortality is simulated by ORCM, the lethal thresholds used may not adequately account for associated changes in dissolved oxygen. Scouring mortality acting on redds during extreme flow events is another possible factor that may be underrepresented.

The research team found empirical models to be useful, both as a means of functionally validating and improving the model, and as tools for imputing missing field measurements. The team used one empirical model to impute missing RST estimates, and the same could be done for dates on which flows are high, leading to very low capture efficiencies. The methods demonstrated here can be used in future to evaluate other recruitment models against rotary screw trap data for this river and other rivers in California.

Development of predictive models of salmon populations is a very challenging task, because the dependent variables are responding to multiple environmental drivers in space and time. Long-term environmental monitoring data are essential to the development process. However, if monitoring data are to be useful to model development, they should be designed with that use in mind. An ongoing process of iterative improvement in both models and monitoring can be achieved if they are seen as interconnected and managed as such. The Tuolumne River and other tributaries of the San Joaquin River offer important opportunities for improved fish management if we can learn from monitoring and modeling experiences and integrate them more closely.

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7.0 Glossary

ACF	Autocorrelation function
AIC	Akaike's information criteria
CDC	California Data Center
CDFG	California Department of Fish and Game
DD	degree days
DOE	U.S. Department of Energy
Energy Commission	California Energy Commission
EIA	Energy Information Agency (U.S. Department of Energy)
GLS	generalized least squares
MID	Modesto Irrigation District
ORCM	Oak Ridge Chinook salmon Model
PIER	Public Interest Energy Research
RD&D	research, development, and demonstration
RST	rotary screw trap
TID	Turlock Irrigation District
USGS	U.S. Geologic Survey (Department of Interior)

Attachment

Designing Optimal Flow Patterns for Fall Chinook Salmon in a Central Valley, California River

This attachment is availble in a separate volume.